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Biosystematic Studies on the Family Tofieldiaceae IV. Taxonomy of *Tofieldia coccinea* in Japan and Korea Including a New Variety

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To better understand variation in *Tofieldia coccinea* in Japan and Korea, we compared morphological findings with molecular phylogenetic analyses using regions of the plastids *trnK*, *trnL* and *trnL–F* plus the nuclear ITS region of 10 species and 19 samples of *Tofieldia*, including 10 samples of *T. coccinea*. Based on morphology, we recognized seven varieties of *T. coccinea*, var. *coccinea*, var. *kondoi*, var. *gracilis*, var. *kiusiana*, var. *geibiensis*, var. *akkana* and a new variety, var. *dibotrya*, with a panicle (dibotryum). According to the molecular phylogeny, *T. coccinea* vars. *coccinea*, *kondoi*, *gracilis* and *akkana* formed a clade with 57–62% bootstrap support; var. *kiusiana* and var. *dibotrya* were excluded from the clade. The topology supports our recognition of *T. coccinea* vars. *kiusiana* and *dibotrya* as distinct from var. *gracilis*, which is morphologically most similar. The molecular phylogeny also supports the inclusion of *T. coccinea* var. *fauriei* within var. *kondoi*. The name *T. yoshiiana* var. *koreana* (comb. nov.) should be used instead of *T. yoshiiana* var. *kanwonensis*.

Key words: lectotype, molecular phylogeny, new combination, new variety, panicle, taxonomy, *Tofieldia coccinea*, *Tofieldia coccinea* var. *dibotrya*, *Tofieldia yoshiiana* var. *koreana*, Tofieldiaceae

Tofieldia Huds. (Alismatales-Tofieldiaceae; Tamura *et al.* 2004, Chase *et al.* 2006) comprises 12 species (Tamura *et al.* 2010, 2011), among which *T. coccinea* Richardson and *T. pusilla* (Michx.) Pers. are widely distributed in circumboreal and circumarctic regions, while the other 10 species are more or less localized. The distribution range of *T. coccinea* extends south into temperate regions in Japan and Korea, where several varieties of *T. coccinea* are differentiated primarily by plant size and flower / fruit density. In this paper, we focus on the varieties of *T. coccinea* in Japan and Korea.

In Japan, *Tofieldia coccinea* was first identified as *T. nutans* Willd. ex Schult. & Schult. f. (Maximowicz 1867). Ohwi (1953) recognized five varieties under *T. nutans*: var. *nutans*, var. *fusca* (Miyabe & Kudo) Ohwi, var. *gracilis* (Franch. & Sav.) Ohwi, var. *kiusiana* (Okuyama) Ohwi and var. *kondoi* (Miyabe & Kudo) H. Hara. Hultén (1943), however, considered *T. nutans* in Asia (type locality: East Siberia) to be conspecific with *T. coccinea* in North America (type locality: Canada). Hara (1961) agreed with Hultén, recognizing five varieties in Japan under *T. coccinea*: var. *coccinea*, var. *fusca* (Miyabe & Kudo) H. Hara, var. *geibiensis* (M. Kikuchi) H. Hara, var. *kiusiana* (Okuyama) H. Hara and var. *kondoi* (Miyabe & Kudo) H. Hara. Hara (1961) proposed the inclusion of var. *gracilis* within var. *kondoi*.

Kitamura (1964) recognized *Tofieldia coccinea* var. *akkana* (T. Shimizu) T. Shimizu in addition to vars. *coccinea*, *geibiensis*, *kiusiana* and *kondoi* (= *T. gracilis*) in Japan, without recognizing *T. coccinea* var. *fusca*. The possibility of this nonrecognition of var. *fusca* had been implied by

Kawano (1961) and Hara (1961). Satake (1982) followed Kitamura's (1964) treatment, but contrary to the then current opinion, Shimizu (1983) distinguished again *T. coccinea* var. *gracilis* (Franch. & Sav.) T. Shimizu from *T. coccinea* var. *kondoi*.

Yamazaki (2002) also recognized *Tofieldia coccinea* var. *gracilis* in addition to var. *coccinea* and var. *kondoi* in Japan, while merging *T. coccinea* var. *akkana*, var. *geibiensis* and var. *kiusiana* with *T. coccinea* var. *gracilis*. Contrary to previous opinions (Matsumura 1905, Miyabe and Kudo 1914, Ohwi 1953, Shimizu 1958, 1983, Hara 1961, Kitamura 1964, Satake 1982) that var. *coccinea* (= var. *nutans*) is distributed northward from Honshu (alpine zone), Yamazaki (2002) confined the distribution to regions northward from central Hokkaido. Thus, the delimitation of varieties of *T. coccinea* in Japan has been quite confused.

In Korea, *Tofieldia fauriei* H. Lév. & Vaniot and *T. taquetii* H. Lév. & Vaniot were described from Jejudo Island (Léveillé 1908) and were subsequently recognized by Nakai (1911). In 1914, however, Nakai reduced *T. taquetii* to *T. fauriei* in a report on plants from Jejudo and Wando Islands. In 1916, Nakai listed *Tofieldia nutans* in a report on plants from Rhobong, Pyeonganbukdo. Chung (1957) recognized *T. fauriei* (= *T. taquetii*) and *T. nutans* in Korea.

Hara (1961) further reduced *T. fauriei* (= *T. taquetii*) to *T. coccinea* var. *kondoi*, and recognized two varieties under *T. coccinea* in Korea, *coccinea* (= *T. nutans*) and *kondoi*. W. T. Lee (1996) accepted Hara's taxonomy, but Y. N. Lee (1996) recognized *T. fauriei* in addition to *T. coccinea*. Yamazaki (2002) considered the difference between *T. coccinea* and *T. fauriei* to be at the infraspecific level and proposed the name *T. coccinea* var. *fauriei* (H. Lév. & Vaniot) T. Yamaz. and also recognized a new variety *T. coccinea* var. *kanwonensis* T. Yamaz. Variety *kanwonensis*, however, was shown by Tamura *et al.* (2011) to belong to *T. yoshiiana* Makino.

Tofieldia coccinea was also reported from Kamchatka by Ledebour (1852), from Shumshu Isl. in the Kuriles (as *T. nutans*) by Yabe and Yendo (1904) and from Sakhalin (as *T. nutans*) by Miyabe and Kudo (1914). It was reported from Ussuri (as *T. nutans*) by Kuzeneva (1935), but not by Regel (1861). Only var. *coccinea* has been reported from those regions.

In this study, we based our first conclusions on the taxonomy of *Tofieldia coccinea* in Japan and Korea on morphological observations, then tested our findings by molecular phylogenetic analyses. In the course of the study, we discovered a new variety of *T. coccinea* from Tanzawa, Kanagawa Pref., Japan, with a panicle (dibotryum), which we describe as *T. coccinea* var. *dibotrya*.

Materials and Methods

Morphological observations

Specimens in the herbaria EWH, HYO, KPM, KYO, MAK, OSA, SAPS, TI and TNS were examined to circumscribe precisely the varieties of *Tofieldia coccinea* in Japan and Korea and to determine whether plants of *Tofieldia* from Tanzawa with panicles and distinct lateral branches were taxonomically distinct. We also created a key to the varieties of *Tofieldia coccinea* in Japan and Korea based on herbarium specimens.

Molecular phylogenetic analyses

DNA sequences of plastid *trnK* (including *matK*), *trnL* and *trnL–F* regions and the nuclear internal transcribed spacer (ITS) region of six varieties and seven samples of *Tofieldia coccinea* determined in this study have been deposited in the DNA Data Bank of Japan (DDBJ) (Table 1). These new sequence data were subsequently included in the matrix of *trnK*, *trnL*, *trnL–F* and ITS sequences of 10 *Tofieldia* species (including 2 varieties and 3 samples from *T. coccinea*) generated by Tamura *et al.* (2010, 2011) (Table 1). Among the 10 species, *T. calyculata* Wahlb., *T. glabra* Nutt., *T. okuboi* Makino and *T. pusilla* were used as an outgroup because the remaining six species (i.e. *T. coccinea*, *T. divergens* Bureau & Franch., *T. furusei* (Hiyama) M. N. Tamura & Fuse, *T. nuda* Maxim., *T. thibetica* Franch. and *T. yoshiiana*) have always formed a clade with 100%

TABLE 1. Sources of materials of *Tofieldia*.

Taxon	Locality	Voucher	Acc. no. (*trnK*)	Acc. no. (*trnL & trnL–F*)	Acc. no. (ITS)
Tofieldia calyculata Wahlb.	Italy: Lago di Garda, Val di Vesta, 550 m	*Vleminckx F. 643* (MO)	AB541029	AB451579	AB541080
T. coccinea Richardson					
var. *coccinea*	USA: Alaska, Lime Hills, 550-670 m	*C. L. Parker & R. Lipkin 8884* (MO)	AB541031	AB451586	AB541082
	Japan: Hokkaido, Mt. Yubari, 1235 m	*M. N. Tamura & S. Fuse 15209* (KYO)	AB746433**	AB746440**	AB746447**
var. *akkana* (T. Shimizu) T. Shimizu	Japan: Iwate Pref., Akka	*Y. Horii s.n.* (KYO)	AB746434**	AB746441**	AB746448**
var. *dibotrya* M. N. Tamura & Fuse var. nov.	Japan: Kanagawa Pref., Tanzawa	*M. N. Tamura 20324* (KYO)	AB746435**	AB746442**	AB746449**
var. *fauriei* (H. Lév. & Vaniot) T. Yamaz.	Korea: Gyeongsangnam-do, Mt. Gaya, 1400 m	*N. S. Lee NS0009182* (EWH)	AB746436**	AB746443**	AB746450**
	Korea: Jeju-do, Mt. Halla, 1600 m	*S. M. Eum Eum0309142* (EWH)	AB746437**	AB746444**	AB746451**
var. *gracilis* (Franch. & Sav.) T. Shimizu	Japan: Akita Pref., Dakigaeri	*K. Hayashi s.n.* (KYO)	AB746438**	AB746445**	AB746452**
var. *kiusiana* (Okuyama) H. Hara	Japan: Miyazaki Pref., Mt. Dohdake	*S. Kurogi & T. Minamitani s.n.*(KYO)	AB746439**	AB746446**	AB746453**
var. *kondoi* (Miyabe & Kudo) H. Hara	Japan: Hokkaido, Mt. Apoi, 635 m	*M. N. Tamura & S. Fuse 15227* (KYO)	AB541032	AB541061	AB541083
	Japan: Nagano Pref., Mt. Amakazari, 1950 m	*M. N. Tamura, S. Fuse & T. Ishii 14344* (KYO)	AB541033	AB541062	AB541084
T. divergens Bureau & Franch.	China: Yunnan, Dali, 2530 m	*M. N. Tamura 4704* (KYO)	AB541034	AB541063	AB541085
T. furusei (Hiyama) M. N. Tamura & Fuse	Japan: Tochigi Pref., Ohya, 165 m	*M. N. Tamura & S. Fuse 20135* (KYO)	AB561166	AB561176	AB561186
T. glabra Nutt.	USA: North Carolina, S of Jacksonville	*H. N. Moldenke 113* (MO)	AB541035	AB451590	AB541086
T. nuda Maxim.	Japan: Mie Pref., Washiyama, 110 m	*M. N. Tamura, S. Fuse & T. Ishii 15171* (KYO)	AB541036	AB541064	AB541087
T. okuboi Makino	Japan: Hokkaido, Mt. Yubari, 1355 m	*M. N. Tamura & S. Fuse 15216* (KYO)	AB541039	AB541067	AB541090
T. pusilla (Michx.) Pers. subsp. *austriaca* H. Kunz	Austria: Mt. Dachstein, 2030 m	*M. N. Tamura & S. Fuse 16074* (KYO)	AB541044	AB541071	AB541095
T. thibetica Franch.	China: Sichuan, Hongya, 1150 m	*C. H. Li 394* (MO)	AB541045	AB451596	AB541096
T. yoshiiana Makino var. *yoshiiana*	Japan: Kagoshima Pref., Yakushima Isl., Kosugidani	*H. Okada s.n.* (OSCU*)	AB561174	AB561184	AB561194

* OSCU = herbarium, Botanical Gardens, Graduate School of Science, Osaka City University.
** DNA sequences that were newly determined in this study.

bootstrap support in earlier studies (Tamura *et al.* 2010, 2011). Using this new matrix, we conducted parsimony and likelihood analyses and constructed molecular phylogenetic trees.

DNA extraction, polymerase chain reaction (PCR) amplification and DNA sequencing were performed as described by Tamura *et al.* (2010). Maximum parsimony (MP) analysis using PAUP* version 4.0 beta 10 (Swofford 2002) was also performed as described by Tamura *et al.* (2010). For maximum likelihood (ML) analysis, the best model of nucleotide evolution was estimated using Modeltest 3.7 (Posada and Crandall 1998). The models selected by the hierarchical likelihood ratio test (hLRT) and Akaike information criterion (AIC) were TrN+G and GTR+I+G, respectively. Both models were implemented in PAUP* as described by Tamura *et al.* (2011). MP bootstrap analysis (1000 replications) and ML bootstrap analysis (100 replications) were performed using PAUP*, as described by Tamura *et al.* (2010, 2011).

Voucher specimens for the molecular phylogenetic analyses were deposited in the herbaria of Kyoto University (KYO), Ewha Womans University (EWH), Museum of Nature and Human Activities, Hyogo (HYO) or the Botanical Gardens, Graduate School of Science, Osaka City University.

Results and Discussion

Morphological observations: recognition of varieties within Tofieldia coccinea *in Japan and Korea*

We recognize seven varieties within *Tofieldia coccinea* in Japan and Korea: *coccinea*, *kondoi*, *gracilis*, *kiusiana*, *geibiensis*, *akkana* and *dibotrya* (var. nov.). The diagnostic characters among the seven varieties include variation in leaf length within the same individual, length of a scape and inflorescence, inflorescence types, pedicel length, tepal length, length ratio of outer tepals to inner ones, anther color, and density and color of capsules. The character states of each variety are listed below under "Artificial key to the varieties of *Tofieldia coccinea* in Japan and Korea".

Our taxonomy agrees with Yamazaki's (2002), the most recent treatment of *Tofieldia coccinea* in Japan and Korea, in recognizing the distribution of var. *coccinea* to be northward from central Hokkaido (Japan) and Pyeonganbuk-do / Pyeongannam-do (Korea) and in recognizing *T. coccinea* var. *gracilis*, but differs from Yamazaki (2002) as follows. Our circumscription of *T. coccinea* var. *kondoi* is wider than Yamazaki's (2002), as it includes *T. coccinea* var. *fauriei*, which Yamazaki (2002) treated as a separate variety. Our circumscription of *T. coccinea* var. *gracilis* is narrower than Yamazaki's (2002), as it excludes *T. coccinea* vars. *kiusiana*, *geibiensis* and *akkana*. We regard the latter three varieties as distinct. We also describe a new variety, *dibotrya*, from Japan.

Morphological observations: a new variety of Tofieldia coccinea

In October 2000, Fuse and Katsuyama collected several individuals of *Tofieldia* from a population in Tanzawa, Kanagawa Pref., Japan, and transplanted them to the nursery of Osaka City University. The cultivated plants consistently produce panicles with distinct lateral branches. *Triantha* (Nutt.) Baker, which is sister to *Tofieldia*, has a reduced panicle with three flowers per node, but lacks branches. *Tofieldia coccinea* var. *gracilis* rarely has two (rarely three) flowers per node, but is unbranched. Panicles with distinct lateral branches have never been reported in *Tofieldia* or *Triantha*. We therefore consider the plants of *Tofieldia* from Tanzawa to be distinct and undescribed. Since the Tanzawa plants differ little from *T. coccinea* var. *gracilis*, which we consider most similar morphologically to the Tanzawa plants, except for the ramification, we regard the Tanzawa plants as a variety of *T. coccinea* and describe it as *T. coccinea* var. *dibotrya*.

Tofieldia coccinea Richardson var. **dibotrya** M. N. Tamura & Fuse, **var. nov.** —Fig. 1

Affinis *Tofieldiae coccineae* var. *gracili*, sed inflorescentia paniculata (dibotrya) diversa.

Typus. JAPAN, Honshu: Kanagawa Pref., Ashigarakami-gun, Yamakita-cho, Tanzawa. Cult. in Osaka City Univ., Japan, 10 Sep. 2010, *M. N. Tamura 20324* (holo-KYO; iso-HYO).

Herbs perennial, glabrous. Rhizome short. Stolons absent. Leaves basal, distichous, basally equitant, unifacial, linear or linear-falcate, 6–14 cm long, 1.2–4 mm broad, variable in length in the same individual, gradually long-acuminate with apex straight or slightly curved, scabrous with small knobby projections on margin; nerves 4–11. Scape with inflorescence 15–25 cm long, with 2 or 3 small sterile leaves; axis reddish brown or green. Inflorescence a panicle (dibotryum), 3–7.5 cm long, branched, 10–55-flowered; longest lateral branch 0.8–2.6 cm long; bracts lanceolate, green. Flowers usually ascending, rarely horizontal, September; pedicel 1.5–5.5 mm long, reddish brown or green; calyculus (epicalyx) 3-lobed. Tepals 6, narrowly oblong, 2.5–3 mm long, white, sometimes reddish brown abaxially. Stamens 6, as long as tepals; filaments white, anthers orange. Pistil 2.8–3.5 mm long, white or

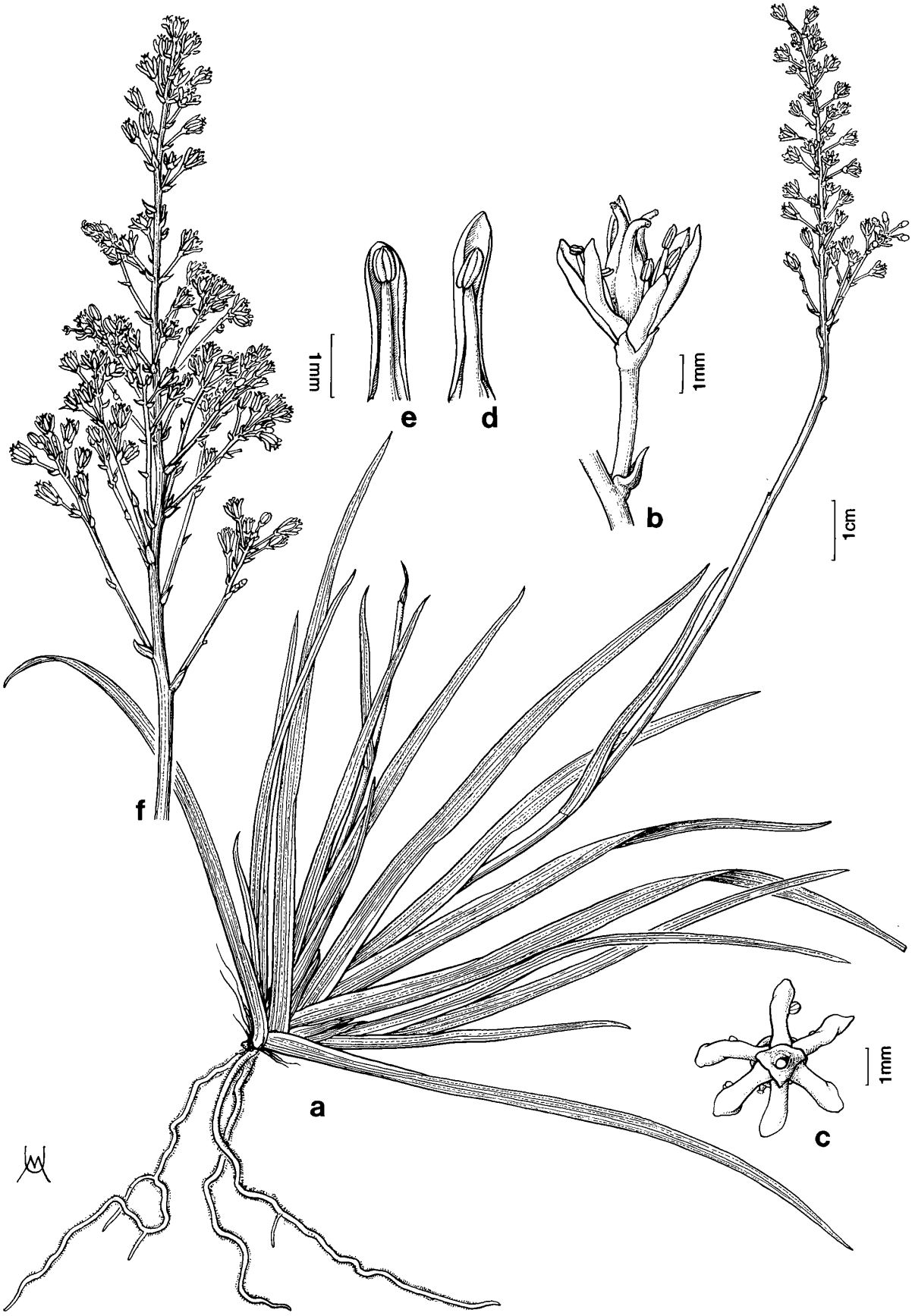

FIG. 1. *Tofieldia coccinea* Richardson var. *dibotrya* M. N. Tamura & Fuse. a, Habit; b, flower in side view; c, flower in back view; d, inner tepal and stamen in adaxial view; e, outer tepal and stamen in adaxial view (M. *N. Tamura 20324*, KYO). f, panicle with distinct lateral branches (*M. N. Tamura & S. Fuse 14899*, KYO).

slightly creamy; ovary superior; styluli 3. Capsules (excluding styluli) ellipsoid, 3–3.8 mm long, ascending, horizontal or descending.

Japanese name. Edauchi-zekishou (nov.).

Distribution and habitat. Known only from the type locality; wet places in crevices of cliffs along streams.

Other specimens examined. JAPAN, Honshu: Kanagawa Pref., Ashigarakami-gun, Yamakita-cho, Tanzawa. Cult. in Osaka City Univ., Japan, *M. N. Tamura & S. Fuse 14899* (KYO), *15472* (KYO), *M. N. Tamura 20148* (KYO).

Molecular phylogenetic analyses: DNA sequence variation within Tofieldia coccinea

The plastid *trnK* genes ranged from 2552 to 2614 bp, with the *matK* gene occupying 1548 bp having three exceptions of 1566 bp in samples of *T. coccinea* var. *coccinea* (from Alaska and Hokkaido) and *T. coccinea* var. *akkana*. The plastid *trnL* gene and *trnL–F* intergenic spacer as well as the nuclear ITS region invariably consisted of 550 bp, 234 bp and 581 bp, respectively. Values of pairwise sequence divergence ranged from up to 0.79% for *trnK*, 0.73% for *trnL* and 0.52% for ITS. DNA sequences of *trnL–F* were exactly the same among the 7 varieties and 10 samples analyzed.

Molecular phylogenetic analyses: topology and information of the trees

In *Tofieldia coccinea* and all of the other samples analyzed in this study, from the 2750-bp aligned length of *trnK*, variable sites comprised 299 bp, among which 92 bp were phylogenetically informative. Of the 583-bp aligned *trnL* sequences, 54 bp were variable, and 21 bp were phylogenetically informative. Of the 267-bp aligned *trnL–F* sequences, 22 bp were variable and 12 bp were phylogenetically informative. Of the 593-bp aligned ITS sequences, 89 bp were variable and 47 bp were phylogenetically informative.

The incongruence length difference (ILD) test among the data sets of the three plastid regions, *trnK*, *trnL* and *trnL–F*, returned a *P* value of 0.25. Considering the incongruence threshold of 0.05, we concluded that the data sets of the three plastid regions were combinable. Furthermore, the *P* value of the ILD test of the combined data set of the three plastid regions and the nuclear ITS data set was 0.14. Therefore, we concluded that the data set of the three plastid regions and nuclear ITS data set were also combinable.

The combined MP analysis of the *trnK* + *trnL* + *trnL–F* + ITS sequences yielded 2835 equally most parsimonious trees of 563 steps. The consistency index (CI) including uninformative characters, retention index (RI) and rescaled consistency index (RC) values for each tree were 0.88, 0.84 and 0.75, respectively.

The topology of the ML tree using the model selected by hLRT was identical with the topology of the ML tree using the AIC model. No incongruence was found when they were compared with the topology of the MP strict consensus tree, except for the clade of *Tofieldia coccinea* var. *kondoi* (Niigata) and *T. coccinea* var. *fauriei*, which formed in the ML trees but collapsed in the MP strict consensus tree (Fig. 2).

According to the MP strict consensus tree as well as the ML trees (Fig. 2), the samples of *Tofieldia coccinea* formed a clade that received 100% bootstrap support. In this clade, *Tofieldia coccinea* var. *coccinea*, var. *kondoi*, var. *fauriei*, var. *gracilis* and var. *akkana* further formed a subclade, although the bootstrap support was weak at 57–62 %. *Tofieldia coccinea* var. *dibotrya* as well as *T. coccinea* var. *kiusiana* were excluded from the subclade.

Tofieldia coccinea var. *dibotrya* is morphologically most similar to *T. coccinea* var. *gracilis*. However, only the latter variety was included in the above subclade; variety *dibotrya* was excluded from it (Fig. 2). This evidence supports our morphological observations that *T. coccinea* var. *dibotrya* is different from *T. coccinea* var. *gracilis* and thus worthy of taxonomic recognition. Likewise, our molecular phylogenetic trees agree with our opinion that *T. coccinea* var. *kiusiana* differs from *T. coccinea* var. *gracilis* (Fig. 2), although Yamazaki (2002) considered var. *kiusiana* to be included within var. *gracilis*.

In the subclade of *Tofieldia coccinea* var. *coccinea*, var. *kondoi*, var. *fauriei*, var. *gracilis* and

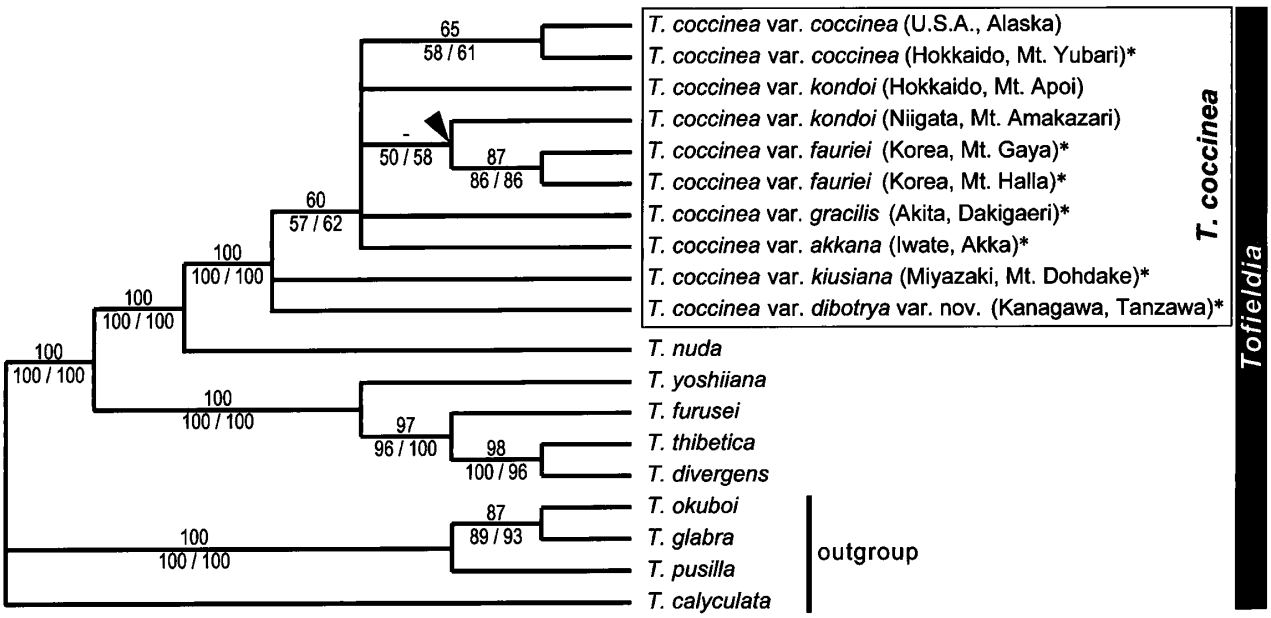

FIG. 2. Strict consensus of 2835 equally most parsimonious trees resulting from the combined maximum parsimony (MP) analysis of the plastids *trnK*, *trnL* and *trnL-F*, and nuclear ITS DNA sequence data from *Tofieldia*. The topology of the maximum likelihood (ML) tree using either of the models [i.e. those selected by hierarchical likelihood ratio test (hLRT) and by Akaike information criterion (AIC)] is identical with the topology of this figure. Arrowhead indicates a branch not present in the MP strict consensus tree. Numbers above branches indicate MP bootstrap values. Numbers below branches indicate ML (hLRT) bootstrap values / ML (AIC) bootstrap values. Accessions with an asterisk were newly included in the molecular phylogenetic analysis.

var. *akkana*, the two samples of *T. coccinea* var. *fauriei* (one from Mt. Gaya on the Korean Peninsula and the other from Mt. Halla on Jejudo Island) were grouped with each other (86–87%). Although Yamazaki (2002) considered *T. coccinea* var. *fauriei* to be endemic to Jejudo Island, our identification of the sample (*N. S. Lee NS0009182, EWH*) from Mt. Gaya, the Korean Peninsula, as *T. coccinea* var. *fauriei* seems to be correct, indicating that *T. coccinea* var. *fauriei* is not only on Jejudo Island but also on the Korean Peninsula.

In the ML trees, the two samples of *Tofieldia coccinea* var. *fauriei* from Korea were further grouped with *T. coccinea* var. *kondoi* from Mt. Amakazari, Niigata, Japan (50–58%), although this grouping collapsed in the MP strict consensus tree. Based on the morphological similarity between *T. coccinea* var. *fauriei* and *T. coccinea* var. *kondoi*, we prefer Hara's (1961) inclusion of var. *fauriei* within *T. coccinea* var. *kondoi*, which does not conflict with the grouping in the ML trees.

Yamazaki (2002) treated *Tofieldia coccinea* var. *coccinea* as being from northern and central Hokkaido in Japan and considered plants from southern Hokkaido to be *T. coccinea* var. *kondoi*. In our molecular phylogenetic analysis, the sample from Mt. Yubari in central Hokkaido was not grouped with the sample from Mt. Apoi in southern Hokkaido but rather with the sample from Alaska, U.S.A. (58–65%), although the geographical distance between Mt. Yubari and Alaska is far greater than that between Mt. Yubari and Mt. Apoi. Thus, Yamazaki's (2002) circumscription of *T. coccinea* var. *coccinea* is supported by our molecular phylogenetic results as well as our morphological ones.

Based on specimens in the KPM herbarium, *Tofieldia coccinea* var. *gracilis* is distributed also in Tanzawa, where *T. coccinea* var. *dibotrya* was found. Unfortunately, however, we were unable to obtain samples of it, now of *T. coccinea* var. *geibiensis* for our molecular phylogenetic analyses. Future molecular phylogeographic studies with more samples covering all the varieties and

the whole distribution area of *T. coccinea* are needed to confirm our taxonomy.

Artificial key to the varieties of Tofieldia coccinea *in Japan and Korea*

1a. Inflorescence a panicle, with distinct lateral branches ..... var. *dibotrya*
1b. Inflorescence a simple raceme, very rarely a reduced panicle without any branches 2
2a. Pedicels 0.5–2 mm long; capsules dense, dark brown or blackish brown ..... var. *coccinea*
2b. Pedicels 2–10 mm long; capsules relatively loosely spaced, brown 3
3a. Scape with inflorescence 5–13.5 cm long; pedicels 2–5(–5.5) mm long; leaves subequal in length on same individual ..... var. *kondoi*
3b. Scape with inflorescence 8–30 cm long; pedicels 3–10 mm long; leaves variable in length on same individual 4
4a. Pedicels 3–6 mm long 5
4b. Pedicels 6–10 mm long 6
5a. Scape with inflorescence 8–20 cm long; tepals 2.5–3.5 mm long; anthers purplish ..... var. *gracilis*
5b. Scape with inflorescence 15–30 cm long; tepals 3.5–4 mm long; anthers pale purplish ..... var. *kiusiana*
6a. Outer tepals nearly as long as inner tepals ..... var. *geibiensis*
6b. Outer tepals 1/2–2/3 times as long as inner tepals ..... var. *akkana*

Taxonomic treatment

Tofieldia coccinea Richardson in Franklin, Narr. Journey Polar Sea: 736 (1823). –Type: Canada, Nunavut, at the Arctic Sea near Bathurst Inlet, *anon. s.n.* (holo-BM, digital image BM!).

var. **coccinea** (Fig. 3)

Tofieldia nutans Willd. ex Schult. & Schult. f., Syst. Veg. 7 (2): 1573 (1830) in observ. sub *T. cernua*. –*Type*: Russia, eastern Siberia, *N. Pallas s.n.* (holo-B, digital image B!).

Tofieldia fusca Miyabe & Kudo in Trans. Sapporo Nat. Hist. Soc. 5: 75 (1914). –*Tofieldia nutans* Willd. ex Schult. & Schult. f. var. *fusca* (Miyabe & Kudo) Koidz. in Bot. Mag. (Tokyo) 31: 138 (1917). –*Tofieldia nutans* Willd. ex Schult. & Schult. f. var. *fusca* (Miyabe & Kudo) Ohwi in Bull. Nat. Sci. Mus. Tokyo 33: 68 (1953). –*Tofieldia coccinea* Richardson var. *fusca* (Miyabe & Kudo) H. Hara in J. Jap. Bot. 36: 392 (1961). –*Tofieldia coccinea* Richardson f. *fusca* (Miyabe & Kudo) Q. S. Sun in P. Y. Fu, Clavis Pl. Chinae Boreal.-Orient. ed. 2: 764 (1995). –Type: Japan, Prov. Ishikari (Hokkaido), Mt. Yubari, 7-9 Aug. 1913, *S. Nishida s.n.* (**lectotype** SAPS!, **hic designates**; isolectotype SAPS!). Other syntypes: Japan, Prov. Ishikari (Hokkaido), Mt. Yubari, on grasslands in northern part of the mountain, 6 Aug. 1912, *H. Yanagisawa & A. Hamana s.n.* (SAPS!); Prov. Ishikari (Hokkaido), Mt. Ashiupetnupuri, 3-5 Aug. 1913, *S. Nishida & H. Yanagisawa s.n.* (SAPS!).

Tofieldia fusca Miyabe & Kudo f. *rishiriensis* Miyabe & Kudo in Trans. Sapporo Nat. Hist. Soc. 5: 76 (1914). –*Tofieldia coccinea* Richardson var. *fusca* (Miyabe & Kudo) H. Hara f. *rishiriensis* (Miyabe & Kudo) Sugim., Keys Herb. Pl. Jap. 2: 566 (1973). –Type: Japan, Prov. Kitami (Hokkaido), Isl. Rishiri, Mt. Rishiri, at the summit, Aug. 1899, *T. Kawakami s.n.* (**lectotype** SAPS!, **hic designates**). Another syntype: Japan, Prov. Kitami (Hokkaido), Isl. Rishiri, Mt. Rishiri, at the summit, 3 Aug. 1896, *W. Hirose s.n.* (SAPS!).

Japanese name. Chishima-zekishou.

Korean name. Suk-eun-kkot-jang-po.

Distribution and habitat. Russia (eastward from E Siberia), Mongolia, NE China, Korea (northward from Pyeonganbuk-do / Pyeongannam-do), Japan (northward from C Hokkaido), Alaska, Canada and Greenland. Alpine slopes and rocky places.

Note. One of the syntypes of *Tofieldia fusca* Miyabe & Kudo from Japan, Honshu, Prov. Shinano (Nagano Pref.), Mt. Shirouma, 12 Aug. 1904, *S. Komatsu s.n.* (SAPS!) is *T. coccinea* var. *kondoi*.

var. **kondoi** (Miyabe & Kudo) H. Hara in J. Jap. Bot. 36: 392 (1961). (Fig. 4) –*Tofieldia kondoi* Miyabe & Kudo in Trans. Sapporo Nat. Hist. Soc. 5: 74 (1914). –*Tofieldia fusca* Miyabe & Kudo var. *kondoi* (Miyabe & Kudo) Tatew. in Res. Bull. Exp. For. Hokkaido Univ. 5: 12 (1928). –*Tofieldia nutans* Willd. ex Schult. & Schult. f. var. *kondoi* (Miyabe & Kudo) H. Hara in Bot. Mag. (Tokyo) 52: 559 (1938). –Type: Japan, Prov. Hidaka (Hok-

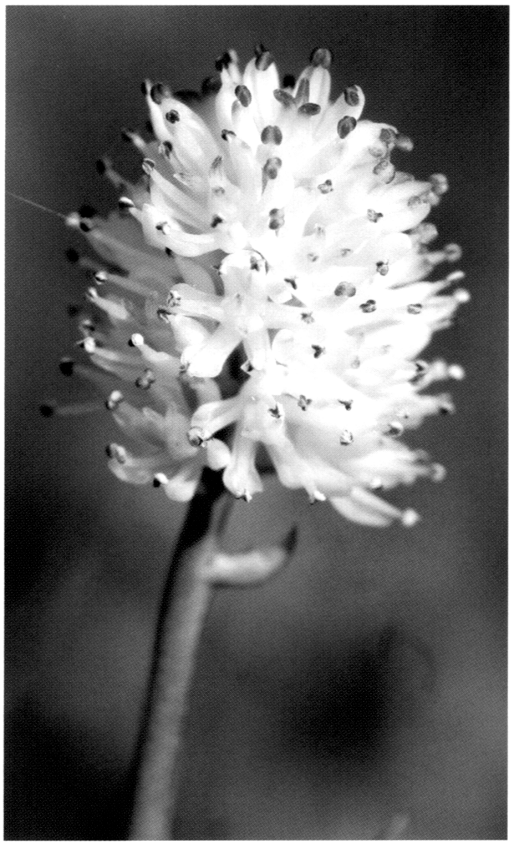

FIG. 3. Dense raceme of *Tofieldia coccinea* Richardson var. *coccinea* from Mt. Yubari, Hokkaido, Japan.

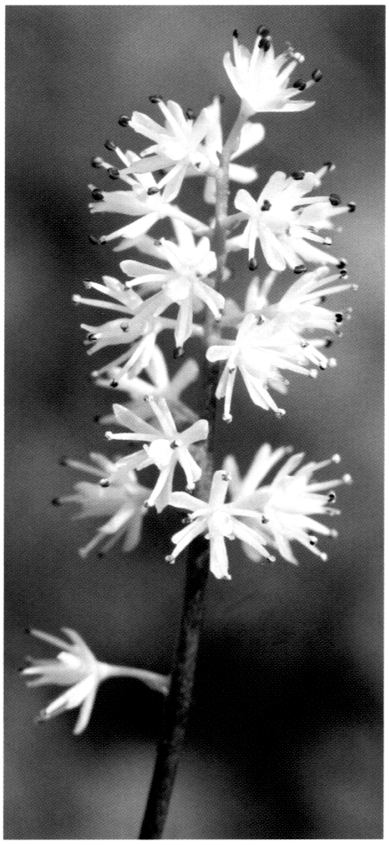

FIG. 4. Slightly loose raceme of *Tofieldia coccinea* Richardson var. *kondoi* (Miyabe & Kudo) H. Hara from Mt. Apoi, Hokkaido, Japan.

kaido), Samani, Mt. Apoi, 17 Aug. 1912, *K. Kondo s.n.* (holo-SAPS!).

Tofieldia fauriei H. Lév. & Vaniot in Repert. Spec. Nov. Regni Veg. 5: 283 (1908). –*Tofieldia coccinea* Richardson var. *fauriei* (H. Lév. & Vaniot) T. Yamaz. in J. Jap. Bot. 77: 302 (2002). –Type: Korea, Jeju-do, Mt. Halla, Aug. 1907, *U. Faurie 2107* (holo-P, digital image P!; iso-KYO!, TI!).

Tofieldia taquetii H. Lév. & Vaniot in Repert. Spec. Nov. Regni Veg. 5: 283 (1908), '*taqueti*'. –Type: Korea, Jeju-do, Mt. Halla, 1700 m, Oct. 1907, *Taquet 404* (**lectotype** P, digital image P!, **hic designates**; isolectotype KYO!). Another syntype: Korea, Jeju-do, 1500 m, Oct. 1906, *U. Faurie 264* (KYO!, P, TI!, digital image P!).

Tofieldia yezoensis Miyabe & Kudo in Trans. Sapporo Nat. Hist. Soc. 5: 73 (1914). –Type: Japan, Prov. Iburi (Hokkaido), Mt. Yeniwa, Aug. 1895, *T. Kawakami s.n.* (holo-SAPS!).

Tofieldia yezoensis Miyabe & Kudo var. *okushirensis* Tatew. in Trans. Sapporo Nat. Hist. Soc. 16: 115 (1940). –Type: Japan, Prov. Shiribeshi (Hokkaido), Isl. Okushiri, the upper Kamoishi River, 10 Aug. 1935, *B. Sonoki s.n.* (holo-SAPS!; iso-SAPS!).

Tofieldia coccinea Richardson f. *pallescens* H. Hara in J. Jap. Bot. 36: 392 (1961). –Type: Japan, Honshu, Prov. Rikuchu (Iwate Pref.), Mt. Iwate, 13 Aug. 1929, *Y. Narita s.n.* (holo-TI!).

Japanese name. Apoi-zekishou.

Korean name. Halla-kkot-jang-po.

Distribution and habitat. Japan (S Hokkaido and N & C Honshu) and Korea (Mt. Gaya on the Korean Peninsula and Mt. Halla on Jejudo Island). Alpine and subalpine slopes and rocky places.

var. **gracilis** (Franch. & Sav.) T. Shimizu, New Alp. Fl. Jap. in Color 2: 358 (1983). (Fig. 5) –*Tofieldia gracilis* Franch. & Sav., Enum. Pl. Jap. 2: 89 (1877), nom. et 531 (1879). –*Tofieldia nutans* Willd. ex Schult. & Schult. f. var. *gracilis* (Franch. & Sav.) Ohwi in Bull. Nat. Sci. Mus. Tokyo 33: 68 (1953). –Type: Japan, in northern mountain, *Sa-*

FIG. 5. Extremely loose raceme of *Tofieldia coccinea* Richardson var. *gracilis* (Franch. & Sav.) T. Shimizu from Dakigaeri, Akita Pref., Japan.

vatier 3749 (holo-P, digital image P!).

Tofieldia sordida Maxim. in Bull. Acad. Sci. St.-Petersb. 11: 437 (1867). –*Tofieldia nutans* Willd. ex Schult. & Schult. f. var. *sordida* (Maxim.) T. Shimizu in Acta Phytotax. Geobot. 17: 153 (1958). –Type: Japan, cult. Yedo (Tokyo), from the neighboring mountain (n.v.).

Tofieldia stenantha Franch. & Sav., Enum. Pl. Jap. 2: 530 (1879). –Type: Japan, in Hakone region, *Savatier 1235* (holo-P, digital image P!).

Japanese name. Chabo-zekishou.

Distribution and habitat. Endemic to Japan: Honshu, Shikoku and Kyushu (Ohita Pref.). On wet, often limestone, rocks.

var. **kiusiana** (Okuyama) H. Hara in J. Jap. Bot. 36: 393 (1961). –*Tofieldia kiusiana* Okuyama in J. Jap. Bot. 26: 294 (1951). –*Tofieldia nutans* Willd. ex Schult. & Schult. f. var. *kiusiana* (Okuyama) Ohwi in Bull. Nat. Sci. Mus. Tokyo 33: 68 (1953). –Type: Japan, Kyushu, Prov. Hyuga (Miyazaki Pref.), Mt. Horagatake (Mt. Dohdake), 23 Aug. 1915, *Z. Tashiro s.n.* (holo-TNS!).

Japanese name. Nagae-chabo-zekishou.

Distribution and habitat. Endemic to Japan: Kyushu (Miyazaki Pref.). At the southern border of the distribution range of *Tofieldia coccinea*. On limestone rocks.

var. **geibiensis** (M. Kikuchi) H. Hara in J. Jap. Bot. 36: 393 (1961). –*Tofieldia kiusiana* Okuyama var. *geibiensis* M. Kikuchi in Ann. Rep. Gakugei Fac. Iwate Univ. 11 (2): 67, f. 2 (1957). –Type: Japan, Honshu, Prov. Rikuchu (Iwate Pref.), Higashi-iwai-gun (Ichinoseki-shi), Geibi-kei, 15 Aug. 1947, *M. Kikuchi s.n.* (holo-IUM; iso-TNS!).

Japanese name. Geibi-zekishou.

Distribution and habitat. Endemic to Japan: Honshu (Iwate Pref.). On limestone cliffs along rivers.

var. **akkana** (T. Shimizu) T. Shimizu in J. Fac. Text. Sci. Technol. Shinshu Univ. 36, ser. A. Biol. 12: 74 (1963). –*Tofieldia akkana* T. Shimizu in Acta Phytotax. Geobot. 17: 153, f. 13 (1958). –Type: Japan, Honshu, Iwate Pref., Shimohei-gun, Iwaizumi-cho, Akka, 15 Oct. 1957, *T. Shimizu 2364* (holo-KYO!).

Japanese name. Akka-zekishou.

Distribution and habitat. Endemic to Japan: Honshu (Iwate Pref.). Limestone crevices and gravelly slopes.

var. **dibotrya** M. N. Tamura & Fuse (Fig. 6) (see above)

Correct name and assignment of Tofieldia coccinea *var.* kanwonensis

Yamazaki (2002) described *Tofieldia coccinea* var. *kanwonensis* based on a specimen

from Gangwon-do, Korea, but Tamura *et al.* (2011) subsequently transferred it to *T. yoshiiana* as *T. yoshiiana* var. *kanwonensis* (T. Yamaz.) M. N. Tamura, Fuse & N. S. Lee. We later found the type specimen of *T. nuda* var. *koreana* Ohwi from Ouen-san, Korea, and noted that the type specimen of *T. nuda* var. *koreana* was included within the range of *T. yoshiiana* var. *kanwonensis* (Tamura *et al.* 2011). As *T. nuda* var. *koreana* was described in 1931 (i.e. earlier than Yamazaki's *T. coccinea* var. *kanwonensis* in 2002), we here propose the new combination, *T. yoshiiana* var. *koreana* (Ohwi) M. N. Tamura, Fuse & N. S. Lee and reduce *T. yoshiiana* var. *kanwonensis* (= *T. coccinea* var. *kanwonensis*) to its synonym.

FIG. 6. Panicle with distinct lateral branches of *Tofieldia coccinea* Richardson var. *dibotrya* M. N. Tamura & Fuse from Tanzawa, Kanagawa Pref., Japan.

Tofieldia yoshiiana Makino var. **koreana** (Ohwi) M. N. Tamura, Fuse & N. S. Lee, **comb. nov.**

Basionym: *Tofieldia nuda* Maxim. var. *koreana* Ohwi in Bot. Mag. (Tokyo) 45: 189 (1931). –Type: Korea, Ouen-san, Aug. 1901, *U. Faurie 696* (holo-KYO!).

Tofieldia coccinea Richardson var. *kanwonensis* T. Yamaz. in J. Jap. Bot. 77: 302 (2002). –*Tofieldia yoshiiana* Makino var. *kanwonensis* (T. Yamaz.) M. N. Tamura, Fuse & N. S. Lee in Taxon 60: 1347 (2011). –Type: Korea, Gangwon-do, Changdo Village, 9 Aug. 1902, *T. Uchiyama s.n.* (holo-TI!).

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